CONTINUOUS AND DISCONTINUOUS VARIA-TIONS AND THEIR INHERITANCE IN PEROMYSCUS. III

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VII. MUTATIONS

In a recent paper (1917a) I have described two widely aberrant color types which have appeared in my cultures, together with certain minor deviations, which likewise seem to behave as discontinuous variations. I am prepared to add considerably to the data thus far published.

1. *"Partial albinos"*

The term albino, as applied to these mice, admittedly does not conform to current usage, and this has become especially evident with the appearance of the mature pelage. I do not think, however, that any of the various names given to fancy races of *Mus musculus* apply to these animals. Having at hand no specimens or even satisfactory colored plates of fancy mice, I am unable to make the comparisons.[27] As previously stated, this mutant strain has red eyes, and lacks pigment wholly on the ears and tail. The fur, on the colored region of the body, is a very·pale gray, rather strongly tinged with a shade of yellow approaching Ridgway's "ochraceous buff," or perhaps "ochraceous orange," on the most highly colored areas. As a convenient non-committal expression, I shall henceforth employ the term "pallid" for these mice."

A microscopic examination of the hairs of these mice reveals some interesting departures from the normal condition:[28] (1) a considerable proportion of the hairs are practically devoid of pigment in the zone which is ordinarily yellow, while the rest are normal in this respect;

[27] It may be that the factional modifications of my mice are the same as those of Castle's "red-eyed yellow" rats (see Castle and Wright, 1915).

[28] Cf. Morgan's account (1911) of the hair of some "modified" individuals of *Peromyscus leucopus ammodytes*.

(2) the surface pigment of the terminal portion of the hairs is nearly or quite lacking; (3) in the basal zone, the black pigment bodies are represented by small flocculent dark masses.   Thus, we are not, as in the next "mutant" to be described, merely dealing with changed proportions of perfectly normal types of hair.   These red-eyed mice possess types which I have not found in any of the rest of my stock.

At the time of my earlier description of these pale sports, no young had been obtained, but their pedigree suggested that they were simple Mendelian recessives. This conjecture has thus far been sustained.   The two " mutants," bred to one another, have given six pale young, like themselves, and no others.   When bred to dark mates, of the same stock as themselves (*sonoriensis-rubidus* hybrids), the pallid animals gave only dark young, except in a single instance where the dark parent was known to be heterozygous.   In this case, one pallid mouse was the outcome.   Of the dark progeny, three broods, aggregating eleven individuals, have thus far been born.

This clear-cut and typical example of Mendelian segregation, in respect to these *mutant* characters, is in striking contrast to the complete lack of segregation— so far as is obvious—in respect to the *subspecific* characters which have entered into the germinal constitution of these same individuals.

As I have previously stated, these parent "mutants" were the offspring of F_1 *sonoriensis-rubidus* hybrids.   In a recent article (1917) the Hagedoorns have described a number of strongly aberrant types of rats (including some waltzers!) which appeared in a mongrel strain resulting from the crossing of *Mus alexandrinus, M. tectorum* and *M. rattus*.   The authors recognize in these aberrant derivations some entirely new products, though they do not attribute their origin to real mutation.   In the opinion of the Hagedoorns, as I understand it, these apparently "mutant" characters have resulted, in each case, from the chance coming together of two recessive factors (or two "absences," according to the prevailing

theory). No two of these ''absences'' coexisted in the gametes of any one of the parent species, and no single ''absence'' by itself is believed to be adequate to produce one of the abnormalities. Since the average number of each kind of ''mutant'' in their stock of 37 was approximately 1 in 16, they assert:

These numbers make it clear that we are not dealing with a sort of period of mutation; it was easy to see that the new types were already given in the genotype of the three species crossed (p. 415).

And in later passages the authors generalize this conjecture, as for example:

The only cause for inheritable variability in multicellular organisms which can be of any account in evolution is mating between individuals of unequal genotype, crossing in the widest sense (Amphimixis) (p. 418).

That the Hagedoorns's explanation does not fit the case of my pallid *Peromyscus* is evident from the history of the stock. I have obtained, in all, 47 F_2 offspring from the mating of F_1 *sonoriensis-rubidus* hybrids, counting only those animals which lived long enough to reveal their essential color characters. These were the progeny of six different fathers and eleven different mothers. Just four of these very pale sports have appeared in my F_2 stock. They are the offspring of a single father by two mothers, both his own sisters. These mothers, by the same father, also produced seven dark young.

It seems plain, therefore, that the mutation in question is not due to any recombination of factors (or their ''absences'') regularly occurring in the parent races. If it were, we should reasonably have expected similar aberrations among the offspring of other parents. It is hard to determine from their published statement the exact pedigree of the Hagedoorn's aberrant rats. But one thing seems plain. All were the progeny of a single father by two mothers, the latter apparently being sisters. The authors are certainly not warranted, therefore, in assuming that such results would have been obtained by mating *any* animals of the same racial composition.

I am inclined to think that my pale red-eyed mice are true mutants, *i. e.,* that they appeared *de novo* in my cul-

tures. It is more than possible, likewise, that the hybridization of such diverse strains was the disturbing element that led to the loss or modification of a ''gene.'' The latter possibility is strengthened by a consideration of the Hagedoorns's waltzing rats and abnormalities of coat color. But this is a very different view from the hypothesis that ''the new types were already given in the genotype of the . . . species crossed.''

2. *Yellow gambeli*

The five normally colored progeny of a single pair of normally colored *Peromyscus maniculatus gambeli* (La Jolla race) became the parents of 21 offspring, of which 14 were normally colored and 7 were of a peculiar yellowish-brown color. These ''mutants,'' which I have called ''yellows,'' are of a shade not very far removed from Ridgway's ''clay color.'' They are considerably darker than some, at least, of the yellow races of *Mus musculus*. Microscopic examination of the hair of these aberrant *gambeli* shows that it is closely similar to that found upon the more highly colored parts of *P. m. sonoriensis*. In comparison with normal specimens of its subspecies the mutant strain is found to have a larger number of the yellow-banded hairs, in proportion to those which are black throughout their entire length. The latter type of hair is, however, by no means wanting. In the second place, the yellow zone of each hair, on the colored parts of the body, occupies, on the average, a considerably larger proportion of its length. On the mid-ventral surface, the basal, plumbeous zone is quite lacking, the hairs being entirely white. Besides the differences stated, I can not be certain of any hair characters which distinguish this type of sports from the normal stock. Moreover, the eyes, ears, tail, etc., carry a normal amount of black pigment.

It is to be noted that these ''yellow'' mice, unlike the ''partial albinos,'' are not distinguished by any types of hair which are lacking in normal individuals. We may, however, very justly regard the yellow condition as having arisen through ''discontinuous variation.'' Though due

merely to a change in the proportion of elements previously present, the new type has arisen abruptly and has diverged so widely that its range of variation does not overlap that of the normal race. Among the many hundreds of individuals which I have dealt with, I have never found any mice which would serve in a true sense to bridge the gap between these two types. Nor have any other yellows appeared in my cultures, except among the descendants of the single pair in question.[29]

As stated in an earlier paper (1917*a*), I trapped several years ago a mouse which I feel fairly certain was a juvenile yellow *gambeli*. It is possible that this character, in a heterozygous condition, may be of not uncommon occurrence among the mice of this vicinity. Thus, the mutation through which my stock came into existence may have taken place among the wild ancestors, many generations earlier. On the other hand, the same genetic instability which led to such a factorial loss or modification in one case may be responsible for its occurrence on many independent occasions. I have no data by which to decide between these two alternatives.

As regards the genetic behavior of these yellow mice, I have fairly satisfactory evidence that they are simple Mendelian recessives. As was stated above, 7 yellows and 14 normal animals constituted the fraternities in which they first appeared. The departure from Mendelian expectation may well have been accidental here, though a differential mortality may possibly have been responsible. The first yellows, bred to their (presumably heterozygous) parents, have given 5 dark and 5 yellow offspring. Bred to homozygous dark animals, they have thus far produced only a single brood, consisting of three dark individuals. Yellows bred to yellows have produced young of the aberrant type only (thus far 10). These frequently do not attain the full yellow color until they as-

[29] Mr. H. H. Collins has, however, found a number of sports of this general appearance among the offspring of a single pair of normally colored individuals which were trapped at La Jolla. Mr. Collins' mice differ somewhat in shade, however, from my ''yellows,'' and may represent a distinct ''mutation.'' His experiments have not been carried far enough to test the genetic behavior of this character.

sume the mature pelage, but I no longer have reason to doubt that the yellow type "breeds true."

A yellow female *gambeli* mated to a "pallid" male of the strain discussed above, has given birth to a single offspring, having abundant dark pigment in the skin, eyes and hair. In other words, these two pale, recessive mutants seem to be "complementary" to one another, as were Castle's two yellow races of rats (Castle and Wright, 1915).

3. *Discontinuous Variation in Restricted Pigment Areas.*

I have discussed briefly elsewhere several sorts of color markings, along with limited data which seemed to show that some of these were inherited in alternative fashion. Other characters of the same type have been added to the list. For example, in the second cage-born generation of *gambeli* I have found three mice with faces strongly "grizzled" by the presence of white hairs. It is probably no mere coincidence that these three grizzled specimens, while not belonging to a single fraternity, are all descended from the same grandparents. Neither the parents nor the grandparents were recorded as having the peculiarity in question, which would hardly have been overlooked if present. Furthermore, the single offspring which I have obtained from a "grizzled" pair exhibits this character plainly, though in a reduced degree. One specimen showing the white-faced condition likewise appeared in the C_2 generation of *sonoriensis*.

Again, occasional mice of perhaps all of the races are characterized by having considerable pigment in the skin of the tail. Normally, the skin of this member is nearly or quite devoid of pigment, the dorsal tail-stripe being due to black hairs. Examination of two successive generations of *rubidus* makes it probable that this caudal skin pigmentation is likewise a hereditary character.

I shall here discuss only one of the localized pigment variations which were dealt with in my earlier report on color "mutations." This is the occurrence of a white-tipped snout, due partly to the absence of skin pigment and partly to the presence in this region of white hairs.

I am now able to indicate rather more definitely the mode of transmission of this character. I wish to lay some stress here upon its genetic behavior, since I regard it as an interesting case in its bearings upon certain theoretical questions.

The pale-nosed condition has been studied only in the darkest of my races, *rubidus*. It was not noticed in the original wild stock, but it may well have been overlooked, as it is not a conspicuous character, and I was not searching for this type of variations when the wild generation was examined. In the first cage-born (''C_1'') generation twelve mice were recorded as having white-tipped snouts, four of the cases being entered as doubtful. At the time of examining these animals I had no idea as to the parentage of the individuals, so that there was no bias in my selection. Upon looking up their pedigrees, I found that ten of the twelve cases (eight certain and two doubtful) were the offspring (indeed, the *only* offspring) of two mothers of the wild generation (P ♀ 40 and 41) by a single father (P ♂ 15). The other two cases (both doubtful) were of other parentage. In connection with the figures just given, it must be stated that the C_1 generation consisted altogether of 60 (surviving) individuals, these being the progeny of twelve females and nine males.

Only 38 mice were obtained in the C_2 generation, 6 of which had white-tipped snouts. As before, the count was made without my being aware of the parentage of the individuals examined. Of the six ''mutants,'' it turned out that four belonged to a fraternity of five, the fifth member of which was normal. This fraternity was the offspring of C_1 ♀ 61 (normal) by C_1 ♂ 10 (white-nosed). The other two mutants were the offspring of this same C_1 ♀ 61, by one of her brothers (♂ 3), the latter being likewise normally pigmented. These parent animals we may believe to have been heterozygous.

Unfortunately, none of the matings of the pale-nosed C_1 individuals *inter se* proved fertile, and indeed the only one of these aberrant mice which left descendants was the ♂ 10 referred to above.

The relationships here indicated, and the incidence of

the aberrant condition, are quite intelligible on the assumption that we have to do with a monohybrid recessive character.   The character can not be dominant, for we had a case of white-nosed young from two dark-nosed parents.   It can not well be due to more than one factor, owing to the relatively large number of recessive individuals.

VIII. Discussion

Any one approaching the data dealt with in the foregoing pages, unhampered by theoretical considerations, would, I think, conclude that we had to do with two types of variation and two types of inheritance, differing from one another in rather fundamental ways.   In the one class we have the continuously graduated differences, occurring within the limits of one of our "subspecies," as well as the differences in average or modal condition which distinguish the various subspecies from one another.   Here we find a sensible *continuity,* both within and between these rather artificial assemblages of individuals, and distinct taxonomic units can be recognized only if we erect more or less arbitrary boundaries.   In heredity, likewise, we have no indication of a dominance of one step or grade in this series over another, and little to suggest that two of these grades, once united or blended in the offspring, tend to reassert their independence in subsequent generations.

In the other class we have the "sports" or "mutations."   These are distinctly *discontinuous,* in relation to the parent stock, either in the sense that one of the two possesses elements which are altogether lacking in the other, or at least in the sense that the new form has undergone such a change in the proportions of existing elements that its range of variation does not overlap that of the normal race.   Looked at in another light, it is of interest to note that all the mutations which I have discussed, with a single exception, are dependent upon the loss of something.   The red-eyed "pallid" mice have lost most of their black and some of their yellow pigment, the "yellows" have lost much of their black.   The white-tipped tails are due to a loss of part of the dorsal tail-stripe, the

"grizzled" heads likewise to the local loss of hair pigment, while the white snouts have resulted from a loss of pigment both in the skin and hair of the latter region. The single exception among the "mutations" which I have observed in *Peromyscus* is the occasional presence of skin pigment in the tail. Here something has been definitely added to the usual condition.[30]

In heredity, too, these mutant characters, whether negative or positive, behave in distinctly discontinuous fashion. They do not blend, but are either present or absent in their entirety.

Taken at face value, I say, the evidence shows that we have to do here with two different types of variation and two different types of heredity. Now admittedly, the naïve view of such a situation is not necessarily the correct one, else we should be forced to return to the geocentric theory of the solar system. But even in this last instance, the burden of proof most assuredly rested on the man who first asserted that the sun did not move around the earth. And to-day the same burden rests upon those who claim—possibly with truth—that heritable variations are all discontinuous and that blended inheritance is an illusion.

In the few remaining pages of this paper, it is obviously impossible to discuss the various lines of evidence which have been advanced in favor of the Mendelian-mutation-pure-line scheme of things. I think that few would be enthusiastic enough to assert that the case had yet been really proved on evidential grounds. The considerations which are chiefly effective in determining one's adherence to this system of beliefs are doubtless of a more general nature. Thus it is argued that Mendelian inheritance has been shown to hold rigidly throughout a vast range of material, and that, therefore, the "unit-factor" conception is probably of universal application. Or, it is contended that the scheme of things here considered is more

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[30] Even in this case, it is possible that we have to do merely with a "reversion," or return to an ancestral condition. Some other Muridæ (*e. g.*, *Mus musculus*) normally have abundant pigment throughout the skin of their tails.

in harmony with the atomistic principles of physics and
chemistry. ''Unit-factors'' have even been identified
with molecules.

In respect to the pigmental characters of our geo-
graphic races, it has been shown to be probable that in-
sensible gradations occur throughout considerable ranges
of territory. There results a series in which marked
contrasts can be found only by comparing individuals
from widely separated localities. The hypothesis that
the variations in this case are of the Mendelian type
involves the assumption that the subspecific differences
have arisen by a whole succession of small mutations in
the same direction, the number of these mutations being
a function of the distance from some hypothetical center
of dispersal. In a recent paper (1917) Morgan has con-
sidered the question whether there are ''any connections
between the gradations of character in allelomorphic
series and the order in which the characters appear,''
i. e., whether ''the assumed fluctuation of factors is a
sequential process.'' He concludes that, ''as a matter
of fact, there is no such relation known . . . for the ac-
tual evidence from multiple allelomorphs shows that
genes may mutate in all directions and also that extreme
mutations such as white eyes arise suddenly from red
and not by graded steps'' (p. 524). These assertions,
which, it is true, were primarily concerned with the
effects of selection, lend little support to the view that
graded geographic variations have arisen through mu-
tation.

The attempt to explain away the substantial mass of
evidence for permanent gametic blending and the indefi-
nite efficacy of selection by invoking the theory of ''mul-
tiple factors'' is too well known to be reviewed here.
Castle has been the most able and vigorous opponent of
this theory. At present I will merely refer to certain
evidence of my own which, I think, supports such an ex-
planation no better than Castle's.

The dorsal tail-stripe is entirely lacking in a certain
strain of my mutants. This stripeless condition is reces-
sive to the striped one. In crosses with normal mice, the

stripe appears in its full size and intensity.[31]   Neverthe-
less, the stripe itself was shown in the preceding pages
to vary from race to race and from one individual to
another.   *And these variations, both racial and individ-
ual, were found to be hereditary.*

The case, of course, is parallel to that of Castle's
hooded rats.   Since "hoodedness" is recessive to ".self-
color" and reappears in one fourth of the F_2 generation,
Castle argues that it is dependent upon a single unit fac-
tor.   Nevertheless, this factor itself presents hereditary
variations in "potency," since it can be modified indefi-
nitely by selection.   The Mendelian counter-argument is
that "hoodedness" behaves as a unit character in certain
crosses merely because there is some one factor without
which it can not manifest itself *at all*.   The variability in
its *degree of manifestation* is due to the fact that the
hooded pattern is modified by the action of a number of
independent cumulative factors.   The argument seems a
bit scholastic, but we must admit that it is logical and
consistent.

Take another instance.   Here I admit that my evidence
is to some extent inferential at present.   I have given
good grounds for believing that the pigmentless con-
dition of the snout in certain strains of *rubidus* is a
simple recessive trait, dependent upon a single factor (or
its absence).   By this I mean that the pigmentless con-
dition is probably allelomorphic to *any degree of pig-
mentation whatever*.

Now we find, in examining a series of mice, all grada-
tions from those with heavily pigmented snouts to those
in which no pigment is to be discovered with the aid of a
hand lens.   Indeed, there are a few "borderland" cases,
which can be only doubtfully distinguished as pigmented
or unpigmented.   Unfortunately, I have no data showing
whether or not these various gradations are hereditary.
Analogy with the case of the tail-stripe would make it
probable that they are.   Moreover, we do know that those

[31] The fact that this condition of the tail stripe is but one manifestation
of a mutation which has affected the hair pigment of the entire body does
not affect the argument.   It is generally believed that most "unit factors"
manifest themselves in diverse ways.

differences in the mean condition of the snout which distinguish the various local races from one another are hereditary.

Here, too, I am aware that we could argue, with flawless logic, that the pigmentless condition was due to the dropping out of some single factor, without which the formation of snout pigment in *any* quantity was impossible. Each member of the graded series of pigmented snouts we might suppose to be conditioned by the presence of this color factor, together with one to many cumulative factors determining the degree of its manifestation.

Johannsen (1913), Morgan (1915) and others have made much of the increased range of variability which has frequently been met with in the F_2 and subsequent generations, even when appearances otherwise pointed to a permanent blending of types. Recently several writers, particularly MacDowell (1916) and Little (1917), have analyzed some of Castle's data and have reached conclusions directly opposed to his. All of these authors (Castle excepted) hold that increasing range of variability in successive hybrid generations is strong evidence for the hypothesis of multiple factors, and we must grant that a pretty good case can be made out along these lines. The theory runs smoothly until we encounter the awkward class of facts which Johannsen has called by the name of "transgressive splitting," *i. e.,* the ultimate extension of the range of hybrid variability beyond that of both of the parent races combined. These facts would seem to prove too much, despite the ingenious explanation which has been offered by the pan-Mendelians to account for them.

An analysis of my quite limited data furnishes no evidence of an increased variability in the F_2 generation, except where it pretty plainly results from an increase in the amount of actual abnormality, due to the conditions of captivity. In the largest, as well as the most normal of the series, the range of variation actually diminishes when we pass from the F_1 to the F_2 generation. I do not, however, offer the present evidence as conclusive, even for the single case of subspecific hybridization in *Peromyscus*. It should be confirmed by data derived from

more extensive series, consisting of animals which are free from any pathological modifications.

We must urge in passing, however, that evidence of segregation, even if valid, is not necessarily to be accepted as evidence of *complete* segregation.   There is no reason why we might not have *partial* segregation, combined with partial gametic blending, as Castle maintains.

In two recent illuminating articles (1917, 1917*a*), Jennings points out how Mendelian-mutationists of the most extreme school have been driven by their own researches into a position that does not differ, according to any pragmatic test, from the one which they so long have vehemently opposed.   More and ever more minute hereditary differences in the manifestation of a given character are recognized, until the limit of distinguishability is approached.   This state of affairs has been attributed to two causes: (1) hereditary modifications in the constitution of single factors, resulting in the formation of series of gradations, allelomorphic to one another; and (2) the existence of series of independent modifying factors, cumulative in their effects.

As remarked earlier in this paper, the contest has latterly come to resemble that allegorical one of the two knights, fighting upon the opposite sides of the same bi-colored shield.   And yet there would seem to be a difference.   The two knights in the legend were both equally right.   In the present case, if we may judge by every pragmatic consideration, the larger measure of right belongs to those who have contended for the frequent permanent blending of hereditary characters in crossing and the continuous modifiability of these characters through selection.   The finely spun theories of their opponents may help us to symbolize the machinery underlying these phenomena, but the phenomena themselves, and not the theories, are the indubitable realities in the case.

IX. Summary

1. In the preceding pages, the differences, structural and pigmental, which distinguish four geographical races of deer-mice are discussed in some detail.   The pigmental

differences relate to a considerable range of more or less independently varying characters, affecting both the intensity and the extensity of the pigment in the hair and skin. They are found to be, in a general way, correlated with certain elements of the physical environment, while the structural differences do not appear to be so correlated.

2. All of these differences, structural and pigmental, are found to be differences of degree, revealed through a comparison of mean or modal conditions rather than of individual animals. In comparing the less divergent of these races with one another, the frequency polygons for any given character overlap broadly.

3. These subspecific differences, and even the minor differences which distinguish one narrowly localized subrace from the parent form, are found to be hereditary, as evidenced by their persistence when environmental conditions are interchanged.

4. The gradations in certain of these characters by which individuals of the same race differ from one another are found to be strongly hereditary.

5. Hybrids between even the most divergent of these four races are predominantly intermediate in character, both in the F_1 and the F_2 generations. In both of these generations a wide range of variability is exhibited, which, however, is little if any greater in the F_2 than in the F_1.

6. In contrast to the sensibly continuous variation and sensibly blended inheritance shown in respect to these subspecific characters, is the behavior of certain "mutations." Here we meet with typical discontinuous variation, and inheritance of the strictly alternative or Mendelian type. It is insisted that the burden of proof rests upon those who contend that these two types of variation and inheritance are reducible to a single category, that of discontinuity. Anything like a proof of this contention appears to be thus far lacking.

SUPPLEMENTARY NOTE (JULY 23, 1918).

It gives me pleasure to call attention to points of close similarity between certain of the views expressed in the

foregoing pages and ones which have recently been advanced by Gates (1917) and by Goldschmidt (1918); likewise to the resemblance between some of the features of geographic variation which I have described for *Peromyscus* and those which have been observed by Swarth (1918) for certain birds. None of these articles had been published at the time the present paper was written.

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